



# Silicon Regulates Antioxidant Activities of Crop Plants under Abiotic-Induced Oxidative Stress: A Review

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Silicon (Si) is the second most abundant element in soil, where its availability to plants can exhort to 10% of total dry weight of the plant. Si accumulation/transport occurs in the upward direction, and has been identified in several crop plants. Si application has been known to ameliorate plant growth and development during normal and stressful conditions over past two-decades. During abiotic (salinity, drought, thermal, and heavy metal etc) stress, one of the immediate responses by plant is the generation of reactive oxygen species (ROS), such as singlet oxygen ( $^1\text{O}_2$ ), superoxide ( $\text{O}_2^-$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), and hydroxyl radicals (OH), which cause severe damage to the cell structure, organelles, and functions. To alleviate and repair this damage, plants have developed a complex antioxidant system to maintain homeostasis through non-enzymatic (carotenoids, tocopherols, ascorbate, and glutathione) and enzymatic antioxidants [superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX)]. To this end, the exogenous application of Si has been found to induce stress tolerance by regulating the generation of ROS, reducing electrolytic leakage, and malondialdehyde (MDA) contents, and immobilizing and reducing the uptake of toxic ions like Na, under stressful conditions. However, the interaction of Si and plant antioxidant enzyme system remains poorly understood, and further in-depth analyses at the transcriptomic level are needed to understand the mechanisms responsible for the Si-mediated regulation of stress responses.

**Keywords:** oxidative stress, stress response, Si fertilization, biochemical and physiological function, stress in plants

## INTRODUCTION

Silicon (Si) has a strong affinity with oxygen; therefore, it usually exists as silica ( $\text{SiO}_2$ ) under natural conditions (Ma and Takahashi, 2002). It also exists in the form of silicic acid [ $\text{Si}(\text{OH})_4$ ] and silicate ( $\text{xM}_2\text{OySiO}_2$ ), depending upon the soil pH (Epstein, 1999). Si accumulation/transport occurs in the upward direction, and has been identified in several crop plants. Si transporter genes have been identified in rice, barley, and maize roots, which facilitate its absorption from the soil to the shoot area. Subsequently, it stimulates various physiological responses such as growth, development, and optimization of enzymatic activities. Si accumulation in plant normally

occurs from the root to shoot, and its transport process has been identified in several crops such as rice, maize, and barley (Ma et al., 2006; Mitani et al., 2009; Cooke and Leishman, 2011; Yamaji et al., 2012). Two Si transporter genes were identified by Ma et al. (2006) in rice root and was named as low silicon gene 1 (*Lsi1*) and low silicon gene 2 (*Lsi2*). Following this several Si transport genes have been characterized in other crops such as barley (*HvLsi1*, *HvLsi2*) and maize (*ZmLsi1*, *ZmLsi2*; Ma et al., 2006; Mitani et al., 2009; Yamaji et al., 2012). After the absorption of Si from the soil into the root, it gets translocated to the shoot area, where it can stimulate various physiological responses, such as plant growth and development (Epstein, 1999; Hamayun et al., 2010; Kim et al., 2012; Mateos-Naranjo et al., 2015), enzymatic activity (Epstein, 1999; Liang et al., 2003; Gong et al., 2005; Kim et al., 2014a,b,c; Todorova et al., 2014; Abdel-Halim et al., 2017), and gene expression (Ma and Yamaji, 2008; Kim et al., 2014a; Vatansever et al., 2017).

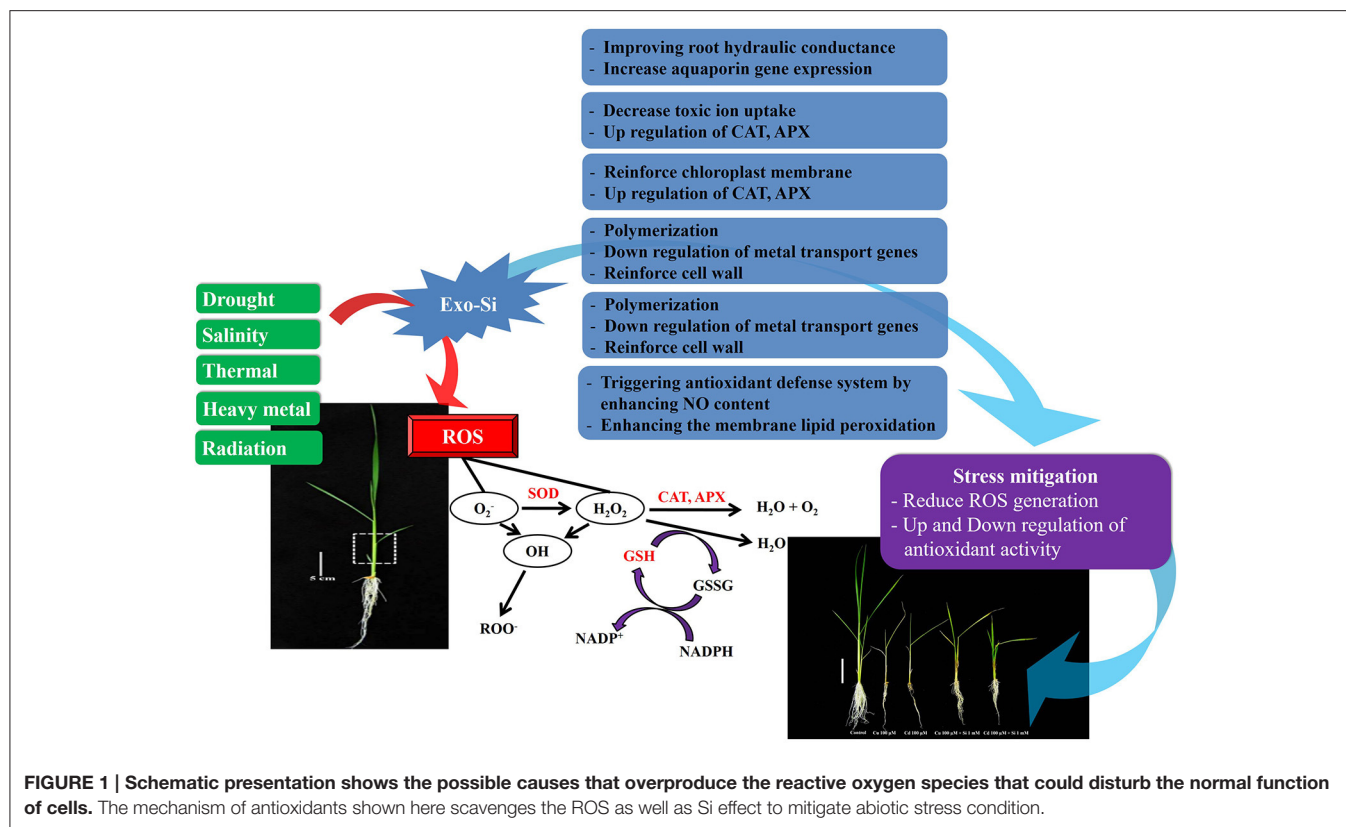
To complete a life cycle, plants are continuously exposed to various abiotic stresses and sometime multifaceted stresses. These stresses in turn causing the generation of various reactive oxygen species (ROS), such as singlet oxygen ( $^1\text{O}_2$ ), superoxide ( $\text{O}_2^-$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), or hydroxyl radicals (OH) in cells (Sharma et al., 2012; Das and Roychoudhury, 2014). These ROS can cause serious oxidative damage to the protein, DNA, and lipids of cell components (Apel and Hirt, 2004; Lobo et al., 2010; Tripathi et al., 2017). Therefore, ROS scavenging is most important defense mechanism to cope with stress condition in plants (Sharma et al., 2012; Baxter et al., 2014; Das and Roychoudhury, 2014). According to previous reports, exogenously Si can improve the ability of ROS scavenging by regulation of antioxidants enzyme activity (Torabi et al., 2015; Kim et al., 2016; Tripathi et al., 2017). Furthermore, regulation pattern across various crop plants is different depending upon the exposure time of the stress (Sharma et al., 2012; Kim et al., 2016). Therefore, here, we discussed various possibilities based on previous literature survey and our understanding the role of Si in modulating antioxidant activities in plants during abiotic stress.

## DEFENSE MECHANISM AGAINST ROS GENERATION

In natural conditions, plants continuously produce several ROS during photosynthesis and respiration processes in cell organelles such as mitochondria, chloroplast, and peroxisomes. Thus, plants can maintain homeostasis by two different detoxification mechanisms involving non-enzymatic and enzymatic antioxidants (Mittler, 2002; Arbona et al., 2003; Apel and Hirt, 2004; Sytar et al., 2013; Wu et al., 2017). In plants, superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are the main enzymatic antioxidants, whereas carotenoids, tocopherols, ascorbate, and glutathione are classified as the non-enzymatic antioxidants (Asada, 1999; Racchi, 2013; Kim et al., 2014b,c). Racchi (2013) reported that SOD exists in various forms, such as Cu/ZnSOD, MnSOD, and FeSOD. Depending upon their affinity with the other ions in

plants, each SOD are distributed in a different form in various plant organs such as chloroplasts (Cu/ZnSOD, FeSOD), cytosol (Cu/ZnSOD), and mitochondria (MnSOD). Primarily, SOD catalyzes the efficient removal of superoxide free radicals in chloroplasts as they are mainly generated in the photosystem I during the light reaction. CAT is located in the peroxisomes of plant cells, and its main role is the elimination of  $\text{H}_2\text{O}_2$ , which is produced by the SOD reaction. Another antioxidant, APX, also can remove  $\text{H}_2\text{O}_2$ ; however, it is distributed in the peroxisomes as well as chloroplasts, cytosol, and mitochondrion (Racchi, 2013). Thus, APX can be found in different forms, such as cAPX (cytosol), mitAPX (mitochondria), sAPX (chloroplast stroma), mAPX (peroxisomes and glyoxisomes), and tAPX (chloroplast thylakoids) depending upon its location (Racchi, 2013). In the chloroplast, APX exist as sAPX and tAPX; the ratio of sAPX and tAPX in chloroplast differs according to the plant species and leaf senescence, and reveals different plant sizes (Sun et al., 2010). The cAPX is located in cytosol; thus, it plays a role in the elimination of  $\text{H}_2\text{O}_2$ , which is generated in cytosol. Therefore, all APXs are different in characteristics such as size, location, role, and amino acid sequences (Caverzan et al., 2012).

Plants can induce defense responses against oxidative stress by activating the non-enzymatic antioxidants, which represent the second line of defense against ROS, hydrophilic molecules (ascorbate, glutathione), and lipophilic metabolites (carotenoids,  $\alpha$ -tocopherol; Racchi, 2013; Suzuki et al., 2014; Gawayed et al., 2017). Ascorbate is a water-soluble antioxidant synthesized in mitochondria. It can translocate to other cell compartments by two different pathways. Normally, ascorbate can directly scavenge ROS ( $^1\text{O}_2$ ,  $\text{O}_2^-$ , and OH) in the cell. Furthermore, it is connected with the de-epoxidase enzyme of violaxanthin, and acts as response matrix of APX (Szarka et al., 2013). Due to its various roles, ascorbate is considered as the most powerful antioxidant in the plant cell (Gill and Tuteja, 2010; Racchi, 2013; Suzuki et al., 2014). Glutathione is also an important water-soluble antioxidant, and plays an important role in scavenging  $^1\text{O}_2$  and OH from chloroplasts (Sharma et al., 2012). In addition, glutathione protects the thiol-groups of enzymes located in the chloroplast stroma and participates in the production of  $\alpha$ -tocopherol and ascorbate (Xiang and Oliver, 1998; Hicks et al., 2007; Sharma et al., 2012; Racchi, 2013). Besides its role in detoxification of ROS, glutathione induces physiological responses such as the regulation of sulfur transport and expression of stress defense genes (Noctor et al., 2002; Racchi, 2013). Carotenoids are a class of phenolic compounds distributed in various fruits and vegetables (Racchi, 2013). They can prevent lipid peroxidation by scavenging single oxide radical from chloroplasts (Kühlbrandt et al., 1994). Carotenoids are synthesized in plastids and consist of 40-carbon isoprenoids. According to Lu and Li (2008), carotenoids are classified as carotenes, which include the carbon and hydrogen atoms, and xanthophylls that contain the oxygenated form of carotenes (Wu et al., 2017). The most important role of  $\alpha$ -tocopherol is that it can eliminate  $^1\text{O}_2$ ,  $\text{O}_2^-$ , and OH free radicals, which are generated in the thylakoid membranes; thus, it can prevent lipid peroxidation (Fryer, 1992; Kataria, 2017).  $\alpha$ -tocopherol has adequate fluidity, enabling it to move easily within the lipid



**FIGURE 1 |** Schematic presentation shows the possible causes that overproduce the reactive oxygen species that could disturb the normal function of cells. The mechanism of antioxidants shown here scavenges the ROS as well as Si effect to mitigate abiotic stress condition.

membrane. Thus, membrane safety is induced by the fluidity of  $\alpha$ -tocopherol (Faltin et al., 2010; Racchi, 2013; **Figure 1**).

## SI IN ROS SCAVENGING UNDER ABIOTIC STRESS CONDITIONS

The enzymatic/non-enzymatic antioxidants are involved in the removal of ROS either directly (catalases and peroxidases) or indirectly through the regeneration of the two major redox molecules (ascorbate and glutathione) in the cells (**Figure 1**). Accumulation of these antioxidants suggests a high level of stress conveyed to the plants (Sharma et al., 2012). This could be also assumed that the plant has defended itself from ROS by producing high amount of antioxidant/enzymes. According to Rouhier and Jacquot (2008), Si application in crops during abiotic stress conditions can regulate ROS generation. Here, we investigated via past and current reports that how antioxidant enzymes could regulate after exogenously Si to different plant species during some of the common abiotic stresses (salinity, drought, temperature, wounding, UV, and heavy metal stress).

## SALINITY STRESS

Decrease in water potential due to high concentration of sodium and chloride ions inhibit plant growth and development (Torabi et al., 2015). According to Kim et al. (2014c), the application

of Si in rice plants under salinity significantly decreased the activities of non-enzymatic MDA and enzymatic antioxidants POD, PPO, and CAT on the other hands, Torabi et al. (2015) observed that when they applied Si to borage plant, SOD activity was significantly increased in Si treatment but activity of CAT and APX was slightly decreased in Si application (**Table 1**). However, Shekari et al. (in press) found that activities of CAT, APX, SOD, and POD were highly increased under Si application with NaCl to herbal *Anethum graveolens* plants. Same pattern of SOD, GPX, APX, GR, and CAT activities was observed by Al-aghabary et al. (2005); Liang et al. (2003), and Zhu et al. (2004). The activities were significantly increased in Si applied barley, cucumber, and tomato plants (**Table 1**).

## DROUGHT STRESS

Drought condition cause damage the photosynthetic pigments and disturb balance between ROS production and antioxidants thus overall affecting crop productivity (Iturbe-Ormaetxe et al., 1998; Gong et al., 2005). According to Gong et al. (2005), Si treatment in wheat plants caused high drought tolerance by up-regulating antioxidant activities of CAT, SOD, and GR (**Table 1**). Ma et al. (2016) also suggested that Si supplement wheat plant showed lower lipid peroxidation, glutathione and total flavonoid content whereas increased ascorbate content was observed. Similarly, Shi et al. (2014, 2016) reported that Si supplementation in tomato plants under PEG induced drought

**TABLE 1 | Modulation of antioxidant activities by Si application under various abiotic stresses.**

Abiotic stresses	Silicon effect	Crop plant	References
Salinity	Increased activity of LPO	Barley	Liang et al., 2003
Salinity	Increased activity of SOD, GPX, APX, and GR Decreased activity of ELP and LPO	Cucumber	Zhu et al., 2004
Salinity	Increased activity of SOD and CAT Decreased activity of APX and MDA	Tomato	Al-aghabary et al., 2005
Salinity	Decreased activity of CAT, MDA, POD, and PPO	Rice	Kim et al., 2014c
Salinity	Increased activity of SOD Decreased activity of CAT and APX	Borago	Torabi et al., 2015
Salinity	Increased activity of CAT, APX, SOD, and POD	Dill	Shekari et al., in press
Drought	Increased activity of CAT, SOD, and GR	Wheat	Gong et al., 2005
Drought	Increased ascorbate contents Reduced glutathione and flavonoid contents	Wheat	Ma et al., 2016
Drought	Decreased activity of APX and MDA	Sunflower	Gunes et al., 2008
Drought	Increased activity of SOD and CAT Decreased activity of POD	Tomato	Shi et al., 2014
Drought	Increased activity of SOD and CAT	Tomato	Shi et al., 2016
High Tem.	Increased activity of SOD, APX, and GPX Decreased activity of CAT	<i>Salvia splendens</i>	Soundararajan et al., 2014
Low Tem.	Increased activity of SOD, GSH, APX, MDHAR, GR, and AsA Decreased activity of MDA	Cucumber	Liu et al., 2009
Low Tem.	Increased activity of GSH and AsA Decreased activity of MDA	Maize	Habibi, 2016
Low Tem.	Increased activity of SOD, CAT, and POD Decreased activity of MDA	Turfgrass	He et al., 2010
Mechanical Wounding	Increased activity of CAT, POD and PPO Decreased activity of MDA	Rice	Kim et al., 2016
Ultraviolet-B	Decreased activity of CAT and POD	Soybean	Shen et al., 2010
Ultraviolet-B	Increased activity of SOD and APX Decreased activity of CAT and GPX	Wheat	Tripathi et al., 2017
Heavy metal (Cd)	Decreased activity of MDA	Rice	Kim et al., 2014a
Heavy metal (Mn)	Decreased activity of POD	Cucumber	Maksimović et al., 2012
Heavy metal (Cr)	Increased activity of SOD, GR, and CAT Decreased activity of APX	Pea	Tripathi et al., 2015

APX, ascorbate peroxidase; CAT, catalase; GSH, glutathione reduced form; GR, glutathione reductase; GPX, guaiacol peroxidase; LPO, lipid peroxidase; SOD, superoxide dismutase; ELP, electrolytic leakage percentage; MDA, malondialdehyde; POD, peroxidase; PPO, polyphenol peroxidase; MDHAR, monodehydroascorbate reductase; AsA, ascorbate.

stress caused tolerance via increased SOD and CAT activities as well as improved water uptake ability of roots (**Table 1**). Whilst, Gunes et al. (2008) observed that Si decreased MDA and APX activities in sunflower during drought condition (**Table 1**).

## THERMAL STRESS

Like other abiotic stress factors, thermo (cold and heat) stress may also disturb the balance between ROS and antioxidants activity. Soundararajan et al. (2014) treated *Salvia splendens* with Si under high temperature (35°C), and found that the activities of SOD, APX and GPX were increased and contrarily that of CAT was decreased (**Table 1**). Liu et al. (2009) observed that during low temperature (day/night; 15/8°C), Si applied to hydroponically cultivated cucumber plant were more resistant to chilling stress compared to non-Si application and was attributed to more activated antioxidants such as SOD, GSH, APX, GR,

MDHAR, and AsA (**Table 1**). Almost same tendency of chilling (day/night; 15/5°C) stress tolerance was observed in turf grass as well, after Na<sub>2</sub>SiO<sub>3</sub> fertilization into soil (He et al., 2010; Habibi, 2016; **Table 1**).

## MECHANICAL WOUNDING

Normally, natural wounding stress is caused by herbivory or lodging and these events could increase hydrogen peroxide level inside plant tissues (León et al., 2001). According to Kim et al. (2014a), exogenous Si application in rice plants improved mechanical strength to overcome losses from wounding stress (**Table 1**).

## ULTRAVIOLET-B

Many studies demonstrated that Si application can induce resistance to UV-B stress via physiological and biochemical



process in plants (Tripathi et al., 2017). In particular, when UV-B applied to tropical plants, MDA, POD, SOD, and anthocyanin contents was increased however, they found decreased activity of CAT was measured (Todorova et al., 2014; **Table 1**). According to Tripathi et al. (2017), UV stress was significantly improved at Si and Si nanoparticle (SiNp) applied wheat seedlings. Especially, mitigation effects between Si and SiNp showed that SiNp applied wheat seedling revealed more strong resistance to UV-B stress (**Table 1**). Other study reported that decreased activity of POD and CAT were measured when they applied Si with UV-B stress to soybean plants (Shen et al., 2010; **Table 1**).

## HEAVY METAL STRESS

In addition, during heavy metal stress, Si application can regulate metal transport and prevent damage shown by decreased MDA activity in rice plants (Kim et al., 2016). In cucumber, Si application can ameliorate manganese toxicity observed by decreased POD activity (Maksimović et al., 2012; **Table 1**). Tripathi et al. (2015) applied SiNp with chromium (Cr) to pea seedling after that, they confirmed stress tolerance phenotypes such as enhanced photosynthetic pigments as well as increased activity of SOD, GR, and CAT however, APX activity was decreased (**Table 1**).

## REFERENCES

- Abdel-Halim, M. E., Hegazy, H. S., Hassan, N. S., and Naguib, D. M. (2017). Effect of silica ions and nano silica on rice plants under salinity stress. *Ecol. Eng.* 99, 282–289. doi: 10.1016/j.ecoleng.2016.11.060
- Al-aghabary, K., Zhu, Z., and Shi, Q. (2005). Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities in tomato plants under salt stress. *J. Plant Nut.* 27, 2101–2115. doi: 10.1081/PLN-200034641
- Apel, K., and Hirt, H. (2004). Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu. Rev. Plant Biol.* 55, 373–399. doi: 10.1146/annurev.arplant.55.031903.141701
- Arbona, V., Flors, V., Jacas, J., García-Agustín, P., and Gómez-Cadenas, A. (2003). Enzymatic and non-enzymatic antioxidant responses of Carrizo citrange, a salt-sensitive citrus rootstock, to different levels of salinity. *Plant Cell Physiol.* 44, 388–394. doi: 10.1093/pcp/pcg059
- Asada, K. (1999). The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 50, 601–639. doi: 10.1146/annurev.arplant.50.1.601
- Baxter, A., Mittler, R., and Suzuki, N. (2014). ROS as key players in plant stress signalling. *J. Exp. Bot.* 65, 1229–1240. doi: 10.1093/jxb/ert375
- Caverzan, A., Passaia, G., Barcellos Rosa, S. B., Werner Riveiro, C. W., Lazzarotto, F., and Margis-Pinheiro, M. (2012). Plant responses to stresses: role of ascorbate peroxidase in the zntioxidant protection. *Genet. Mol. Biol.* 35, 1011–1019. doi: 10.1590/S1415-47572012000600016
- Cooke, J., and Leishman, M. R. (2011). Is plant ecology more siliceous than we realise? *Trends Plant Sci.* 16, 61–68. doi: 10.1016/j.tplants.2010.10.003
- Das, K., and Roychoudhury, A. (2014). Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Front Environ Sci.* 2:53. doi: 10.3389/fenvs.2014.00053
- Eppstein, E. (1999). Silicon. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 50, 641–664. doi: 10.1146/annurev.arplant.50.1.641
- Faltin, Z., Holland, D., Velcheva, M., Tchapovsky, M., Roeckel-Drevet, P., Handa, A. K., et al. (2010). Glutathione peroxidase regulation of reactive oxygen species level is crucial for *in vitro* plant differentiation. *Plant Cell Physiol.* 51, 1151–1162. doi: 10.1093/pcp/pcq082
- Fryer, M. J. (1992). The antioxidant effects of thylakoid vitamin E ( $\alpha$ -tocopherol). *Plant Cell Environ.* 15, 381–392. doi: 10.1111/j.1365-3040.1992.tb00988.x
- Gill, S. S., and Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.* 48, 909–930. doi: 10.1016/j.plaphy.2010.08.016
- Gong, H., Zhu, X., Chen, K., Wang, S., and Zhang, C. (2005). Silicon alleviates oxidative damage of wheat plants in pots under drought. *Plant Sci.* 169, 313–321. doi: 10.1016/j.plantsci.2005.02.023
- Gowayed, S. M., Al-Zahrani, H. S., and Metwali, E. M. (2017). Improving the Salinity tolerance in potato (*Solanum tuberosum*) by exogenous application of silicon dioxide nanoparticles. *Int. J. Agric. Biol.* 19, 183–194. doi: 10.17957/IJAB/15.0262
- Gunes, A., Pilbeam, D. J., Inal, A., and Coban, S. (2008). Influence of silicon on sunflower cultivars under drought stress, I: growth, antioxidant mechanisms, and lipid peroxidation. *Commun. Soil Sci. Plant Anal.* 39, 1885–1903. doi: 10.1080/00103620802134651
- Habibi, G. (2016). Effect of foliar-applied silicon on photochemistry, antioxidant capacity and growth in maize plants subjected to chilling stress. *Acta Agric. Slov* 107, 33–43. doi: 10.14720/aas.2016.107.1.04
- Hamayun, M., Sohn, E. Y., Khan, S. A., Shinwari, Z. K., Khan, A. L., and Lee, I. J. (2010). Silicon alleviates the adverse effects of salinity and drought stress on growth and endogenous plant growth hormones of soybean (*Glycine max* L.). *Pak. J. Bot.* 42, 1713–1722.
- He, Y., Xiao, H., Wang, H., Chen, Y., and Yu, M. (2010). Effect of silicon on chilling-induced changes of solutes, antioxidants, and membrane stability in seashore paspalum turfgrass. *Acta Physiol. Plant* 32, 487–494. doi: 10.1007/s11738-009-0425-x
- Hicks, L. M., Cahoon, R. E., Bonner, E. R., Rivard, R. S., Sheffield, J., and Jez, J. M. (2007). Thiol-based regulation of redox-active glutamate-cysteine ligase

## CONCLUSIONS

During abiotic stress conditions, the Si application shows varying response to ROS scavenging by activating the defense system plants. In doing so, the activity of antioxidant arsenals (CAT, SOD, PPO, POD, APX, GPX, and GSSH) may also oscillate depending upon the intensity of stress and plant type. Si supplemented plants showed resistance to abiotic stress through, lowering ROS production by (i) enhancing CAT and APX activities as both are involved in conversion of  $H_2O_2$  into  $H_2O$  (ii) and decreasing MDA activity.

## AUTHOR CONTRIBUTIONS

YK wrote the manuscript; MW and AK contributed in drafting and revising manuscript; IL draw the figure and revised the manuscript.

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- from *Arabidopsis thaliana*. *Plant Cell* 19, 2653–2661. doi: 10.1105/tpc.107.052597
- Iturbe-Ormaetxe, I., Escuredo, P. R., Arrese-Igor, C., and Becana, M. (1998). Oxidative damage in pea plants exposed to water deficit or paraquat. *Plant Physiology* 116, 173–181. doi: 10.1104/pp.116.1.173
- Kataria, S. (2017). “Chapter 6: Oxidative stress and antioxidative defence system in plants in response to UVB stress,” in *UV-B Radiation: From Environmental Stressor to Regulator of Plant Growth*, eds V. P. Singh, S. Singh, S. M. Prasad, and P. Parihar (New York, NY: John Wiley & Sons), 99–122.
- Kühlbrandt, W., Wang, D. N., and Fujiyoshi, Y. (1994). Atomic model of plant light-harvesting complex by electron crystallography. *Nature* 367, 614–621. doi: 10.1038/367614a0
- Kim, Y. H., Khan, A. L., Kim, D. H., Lee, S. Y., Kim, K. M., Waqas, M., et al. (2014a). Silicon mitigates heavy metal stress by regulating P-type heavy metal ATPases, *Oryza sativa* low silicon genes, and endogenous phytohormones. *BMC Plant Biol.* 14:13. doi: 10.1186/1471-2229-14-13
- Kim, Y. H., Khan, A. L., Shinwari, Z. K., Kim, D. H., Waqas, M., Kamran, M., et al. (2012). Silicon treatment to rice (*Oryza sativa* L. cv. ‘Gopumbyeo’) plants during different growth periods and its effects on growth and grain yield. *Pak. J. Bot.* 44, 891–897.
- Kim, Y. H., Khan, A. L., Waqas, M., Jeong, H. J., Kim, D. H., Shin, J. S., et al. (2014b). Regulation of jasmonic acid biosynthesis by silicon application during physical injury to *Oryza sativa* L. *J. Plant Res.* 127, 525–532. doi: 10.1007/s10265-014-0641-3
- Kim, Y. H., Khan, A. L., Waqas, M., Shahzad, R., and Lee, I. J. (2016). Silicon-mediated mitigation of wounding stress acts by up-regulating the rice antioxidant system. *Cereal Res. Commun.* 44, 111–121. doi: 10.1556/0806.43.2015.031
- Kim, Y. H., Khan, A. L., Waqas, M., Shim, J. K., Kim, D. H., Lee, K. Y., et al. (2014c). Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. *J. Plant Growth Regul.* 33, 137–149. doi: 10.1007/s00344-013-9356-2
- León, J., Rojo, E., and Sánchez Serrano, J. J. (2001). Wound signalling in plants. *J. Exp. Bot.* 52, 1–9. doi: 10.1093/jxb/52.354.1
- Liang, Y., Chen, Q., Liu, Q., Zhang, W., and Ding, R. (2003). Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). *J. Plant Physiol.* 160, 1157–1164. doi: 10.1078/0176-1617-01065
- Liu, J. J., Lin, S. H., Xu, P. L., Wang, X. J., and Bai, J. G. (2009). Effects of exogenous silicon on the activities of antioxidant enzymes and lipid peroxidation in chilling-stressed cucumber leaves. *Agr. Sci. China* 8, 1075–1086. doi: 10.1016/S1671-2927(08)60315-6
- Lobo, V., Patil, A., Phatak, A., and Chandra, N. (2010). Free radicals, antioxidants and functional foods: impact on human health. *Pharmacogn Rev.* 4, 118–126. doi: 10.4103/0973-7847.70902
- Lu, S., and Li, L. (2008). Carotenoid metabolism: biosynthesis, regulation, and beyond. *J. Integr. Plant Biol.* 50, 778–785. doi: 10.1111/j.1744-7909.2008.00708.x
- Ma, D., Sun, D., Wang, C., Qin, H., Ding, H., Li, Y., et al. (2016). Silicon application alleviates drought stress in wheat through transcriptional regulation of multiple antioxidant defense pathways. *J. Plant Growth Regul.* 35, 1–10. doi: 10.1007/s00344-015-9500-2
- Ma, J. F., and Takahashi, E. (2002). *Soil, Fertilizer, and Plant Silicon Research in Japan*. Amsterdam: Elsevier.
- Ma, J. F., Tamai, K., Yamaji, N., Mitani, N., Konishi, S., Katsuhara, M., et al. (2006). A silicon transporter in rice. *Nature* 440, 688–691. doi: 10.1038/nature04590
- Ma, J. F., and Yamaji, N. (2008). Functions and transport of silicon in plants. *Cell Mol. Life Sci.* 65, 3049–3057. doi: 10.1007/s00018-008-7580-x
- Maksimović, J. D., Mojović, M., Maksimović, V., Römhild, V., and Nikolic, M. (2012). Silicon ameliorates manganese toxicity in cucumber by decreasing hydroxyl radical accumulation in the leaf apoplast. *J. Exp. Bot.* 63, 2411–2420. doi: 10.1093/jxb/err359
- Mateos-Naranjo, E., Galle, A., Florez-Sarasa, I., Perdomo, J. A., Galmés, J., Ribas-Carbo, M., et al. (2015). Assessment of the role of silicon in the Cu-tolerance of the C 4 grass *Spartina densiflora*. *J. Plant Physiol.* 178, 74–83. doi: 10.1016/j.jplph.2015.03.001
- Mitani, N., Chiba, Y., Yamaji, N., and Ma, J. F. (2009). Identification and characterization of maize and barley Lsi2-like silicon efflux transporters reveals a distinct silicon uptake system from that in rice. *Plant Cell* 21, 2133–2142. doi: 10.1105/tpc.109.067884
- Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* 7, 405–410. doi: 10.1016/S1360-1385(02)02312-9
- Noctor, G., Gomez, L., Vanacker, H., and Foyer, C. H. (2002). Interactions between biosynthesis, compartmentation and transport in the control of glutathione homeostasis and signaling. *J. Exp. Bot.* 53, 1283–1304. doi: 10.1093/jxb/53.7.1283
- Racchi, M. L. (2013). Antioxidant defenses in plants with attention to *Prunus* and *Citrus* spp. *Antioxidants* 2, 340–369. doi: 10.3390/antiox2040340
- Rouhier, N., and Jacquot, J. P. (2008). Getting sick may help plants overcome abiotic stress. *New Phytol.* 180, 738–741. doi: 10.1111/j.1469-8137.2008.02673.x
- Sharma, P., Jha, A. B., Dubey, R. S., and Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J. Bot.* 2012:217037. doi: 10.1155/2012/217037
- Shekari, F., Abbasi, A., and Mustafavi, S. H. (in press). Effect of silicon and selenium on enzymatic changes and productivity of dill in saline condition. *J. Saudi Soc. Agric. Sci.* doi: 10.1016/j.jssas.2015.11.006
- Shen, X., Zhou, Y., Duan, L., Li, Z., Eneji, A. E., and Li, J. (2010). Silicon effects on photosynthesis and antioxidant parameters of soybean seedlings under drought and ultraviolet-B radiation. *J. Plant Physiol.* 167, 1248–1252. doi: 10.1016/j.jplph.2010.04.011
- Shi, Y., Zhang, Y., Han, W., Feng, R., Hu, Y., Guo, J., et al. (2016). Silicon enhances water stress tolerance by improving root hydraulic conductance in *Solanum lycopersicum* L. *Front. Plant Sci.* 7:196. doi: 10.3389/fpls.2016.00196
- Shi, Y., Zhang, Y., Yao, H., Wu, J., Sun, H., and Gong, H. (2014). Silicon improves seed germination and alleviates oxidative stress of bud seedlings in tomato under water deficit stress. *Plant Physiol. Biochem.* 78, 27–36. doi: 10.1016/j.plaphy.2014.02.009
- Soundararajan, P., Sivasenan, I., Jana, S., and Jeong, B. R. (2014). Influence of silicon supplementation on the growth and tolerance to high temperature in *Salvia splendens*. *Hort. Environ. Biotechnol.* 55, 271–279. doi: 10.1007/s13580-014-0023-8
- Sun, W. H., Duan, M., Shu, D. F., Yang, S., and Meng, Q. W. (2010). Over-expression of tomato tAPX gene in tobacco improves tolerance to high or low temperature stress. *Biol. Plant* 54, 614–620. doi: 10.1007/s10535-010-0111-2
- Suzuki, N., Rivero, R. M., Shulaev, V., Blumwald, E., and Mittler, R. (2014). Abiotic and biotic stress combinations. *New Phytol.* 203, 32–43. doi: 10.1111/nph.12797
- Sytar, O., Kumar, A., Latowski, D., Kuczyńska, P., Strzałka, K., and Prasad, M. N. V. (2013). Heavy metal-induced oxidative damage, defense reactions, and detoxification mechanisms in plants. *Acta Physiol. Plant* 35, 985–999. doi: 10.1007/s11738-012-1169-6
- Szarka, A., Bánhegyi, G., and Asard, H. (2013). The inter-relationship of ascorbate transport, metabolism and mitochondrial, plastidic respiration. *Antioxid Redox Signal.* 19, 1036–1044. doi: 10.1089/ars.2012.5059
- Todorova, D., Sergiev, I., Moskova, I., Katerova, Z., Georgieva, N., Alexieva, V., et al. (2014). Biochemical responses of triticales plants treated with UV-B irradiation and nutrient solution enriched with humic acids. *Turkish J. Bot.* 38, 747–753. doi: 10.3906/bot-1312-52
- Torabi, F., Majd, A., and Enteshari, S. (2015). The effect of silicon on alleviation of salt stress in borage (*Borago officinalis* L.). *Soil Sci. Plant Nut.* 61, 788–798. doi: 10.1080/00380768.2015.1005540
- Tripathi, D. K., Singh, S., Singh, V. P., Prasad, S. M., Dubey, N. K., and Chauhan, D. K. (2017). Silicon nanoparticles more effectively alleviated UV-B stress than silicon in wheat (*Triticum aestivum*) seedlings. *Plant Physiol. Biochem.* 110, 70–81. doi: 10.1016/j.plaphy.2016.06.026
- Tripathi, D. K., Singh, V. P., Prasad, S. M., Chauhan, D. K., and Dubey, N. K. (2015). Silicon nanoparticles (SiNP) alleviate chromium (VI) phytotoxicity in *Pisum sativum* (L.) seedlings. *Plant Physiol. Biochem.* 96, 189–198. doi: 10.1016/j.plaphy.2015.07.026
- Vatansever, R., Ozyigit, I. I., Filiz, E., and Gozukara, N. (2017). Genome-wide exploration of silicon (Si) transporter genes, *Lsi1* and *Lsi2* in plants;

- insights into Si-accumulation status/capacity of plants. *BioMetals* 30, 185–200. doi: 10.1007/s10534-017-9992-2
- Wu, Z., Liu, S., Zhao, J., Wang, F., Du, Y., Zou, S., et al. (2017). Comparative responses to silicon and selenium in relation to antioxidant enzyme system and the glutathione-ascorbate cycle in flowering Chinese cabbage (*Brassica campestris* L. ssp. *chinensis* var. *utilis*) under cadmium stress. *Environ. Exp. Bot.* 133, 1–11. doi: 10.1016/j.envexpbot.2016.09.005
- Xiang, C., and Oliver, D. J. (1998). Glutathione metabolic genes coordinately respond to heavy metals and jasmonic acid in *Arabidopsis*. *Plant Cell* 10, 1539–1550. doi: 10.1105/tpc.10.9.1539
- Yamaji, N., Chiba, Y., Mitani-Ueno, N., and Ma, J. F. (2012). Functional characterization of a silicon transporter gene implicated in silicon distribution in barley. *Plant Physiol.* 160, 1491–1497. doi: 10.1104/pp.112.204578
- Zhu, Z., Wei, G., Li, J., Qian, Q., and Yu, J. (2004). Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). *Plant Sci* 167, 527–533. doi: 10.1016/j.plantsci.2004.04.020
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